# Seasonal Changes in the Behavior and Plasma Titers of Various Hormones in Barheaded Geese, *Anser indicus*

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# Seasonal Changes in the Behavior and Plasma Titers of Various Hormones in Barheaded Geese, *Anser indicus*

By John Philip Dittami

*With 11 figures*

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## Abstract

A number of behavioral and physiological parameters including the circulating levels of 7 hormones were investigated in a free ranging population of barheaded geese in Seewiesen, W. Germany. Behavioral data were collected on the entire flock from which seasonal changes in the frequencies were determined. In addition, data on the behavior of individuals were obtained to aid in the comparison of seasonal changes in behavior and hormones. The resulting curves were used to examine whether the annual changes in the frequencies of various behaviors were related to changes in circulating hormonal concentrations. Lastly, the physiological data were discussed with regard to reproductive biology in birds.

## A. Introduction

The relationship between hormones and behavior is generally investigated in one of two ways. The first is to alter either a hormone's titer or receptor sensitivity and look for changes in behavior, and the second is to simultaneously monitor spontaneous changes of both behavior and hormones. Data from the two approaches can not always be equated. Nonetheless, the results from the second type of study are often recommendable as a pre-requisite for manipulation experiments. Without these baseline data, forced alterations of the hormonal milieu are sometimes difficult to interpret because artifacts and indirect effects can not be ruled out.

Unfortunately, the conclusions which can be drawn from studying correlations between hormonal and behavioral changes are often limited. Many studies only concentrate on one or two hormones, neglecting the influence of

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other possibly relevant endocrine factors. In experiments where annual or seasonal changes have been investigated, the animals have rarely, if ever, been studied in their natural environment while going through a normal reproductive cycle. The problem has been that it is extremely difficult to carry out a comprehensive physiological and behavioral study together on a free living animal because of techniques and facilities required.

From an endocrinological standpoint, many of the difficulties in studying birds have been alleviated. Micro assays have been developed for LH (FOLLETT et al. 1972), prolatin (MCNEILLY et al. 1978) and thyroid hormones (HALL 1979) as well as techniques for separating and analysing a number of steroids in the same plasma sample (WINGFIELD and FARNER 1975). What remains to be done is to couple these techniques to extensive behavioral studies.

The major goal in this study was to gather baseline data on seasonal changes in behavior and hormones in geese. An attempt was made to collect data on as many behavioral and endocrinological parameters as possible on a free living population. The time basis was the annual cycle which in the goose is a chain of seasonally linked occurrences: spring migration — breeding — primary molt — fall migration. Each occurrence is characterized by certain behavioral and physiological features.

Many characteristics of geese render them advantageous subjects for this type of study. Their behaviors are easily recognized and quantified. They have been categorized and interpreted by a number of authors (HEINROTH 1911; HEINROTH and HEINROTH 1922; CHRISTOLEIT 1929; LORENZ 1959; COLLIAS and JAHN 1959; FISCHER 1965, 1972, 1973 a, b; JOHNSGARD 1965; RAVELING 1970; RADESÄTER 1974 a, b; WÜRDINGER 1970, 1975, 1978). Geese are easily tamed and kept in a semi-captive situation where the collection of behavioral data and blood sampling is facilitated. Seasonal patterns of reproduction have been shown to remain intact when geese are exposed to temperature and photoperiodic cycles somewhat different from their natural habitat (DAVIES et al. 1969; MURTON and KEAR 1973, 1976). Lastly, geese are large enough birds to permit the taking of ml blood samples at regular intervals. This enables the investigation of a number of hormone titers in the same plasma sample.

The goose species chosen for this study was the barheaded goose, *Anser indicus*. It is an Asian species which breeds on high elevation lakes between the Tien Shan and Kokonor in the Hymalayas (58°—30° N) and winters primarily in India and Pakistan (ALI 1979). Earlier estimates of goose populations had reckoned it the world's second most populous species (OGILVIE 1978). It is a common species in many waterfowl collections and is the only consistently breeding species on the Eßsee in Seewiesen, where this study was undertaken.

## B. Methods

The colony of free ranging geese in Seewiesen was studied from January 1978 to July 1980. This population as well as the study area have been described in a report by WÜRDINGER

(1972). The composition of the flock in terms of age groups is shown in Table 1. The geese were all-year residents and were provided ad libitum with a bran pellet feed from cages on the edge of the lake. The cages were equipped with trap doors to permit capturing the geese. Crushed corn and, in winter, germinated wheat were scattered on the edge of the lake once a day. The geese nested in boxes on floating platforms which were checked every few days during the breeding season.

*Table 1:* Spring census of the barheaded goose population with respect to age classes

| | 1978 | 1979 | 1980 |
|---|---|---|---|
| Juveniles 1-2 years | 25 | 23 | 29 |
| Subadults 2-3 years | 5 | 15 | 18 |
| Adults over 3 years | 41 | 40 | 49 |
| Families | 9 | 9 | 13 |

## I. Collection of Behavioral Data

Behavioral data were collected on two levels: the frequencies of behaviors in the entire flocks from February 1978 to July 1980 and that of selected individuals from April 1979 to July 1980. All protocols were taken in the morning, 6.00—12.00 h AM. To standardize the protocol situation, data were taken after scattering food on the edge of the lake. The geese were never captured in this situation and therefore tolerated my presence. This had the advantage that they were always present and active during the protocol and that the frequency of interactions between geese was maximized.

### 1. Flock Data

Data on the flock were collected in protocols which lasted 20 min. In total, 420 protocols were taken during the study. Before scattering food, the numbers and groupings of geese in the area were recorded. Individuals within about 10 m of each other were defined as belonging to the same group. The group size was used as a measure of the flock's cohesiveness.

The following behaviors were recorded:

*Pairbond displays:* Triumph ceremonies as have been described for barheaded geese by Johnsgard (1965) and, in addition, bouts of cackling between members of a pair or family were counted. Both behaviors presumably function to strengthen the social bonds and aid the geese in asserting themselves when interacting with others.

*Courting and sexual behavior:* The number and identity of courting geese were recorded. Courting behavior was broken down into two categories: angle necks as described by Lorenz (1959) for greylag geese, and head dipping or precopulatory movements (Johnsgard 1965). Lastly, copulations were counted.

*Intensive aggressive encounters:* Two categories were investigated. Flight *chases* where one goose attacked another and then pursued it in flight were differentiated from *fights* where geese attacked each other and ended up beating each other with their wings. These behaviors have been described for greylag geese by Fischer (1965, 1972).

During these flock protocols, data were collected on the identity of geese sitting in nest boxes or defending them. At the beginning of the molting period, the flock was checked daily to ascertain when the primary molt began for each individual. Flight activity was measured by recording whether sustained flight, longer than 20 s, occurred in an observational period.

### 2. Data from Individual Protocols

Certain pairs of geese belonging to various social classes (see below) were investigated to enable a comparison of hormones and behavior on an individual basis. The protocol situation was identical to that mentioned above except information was only collected on one pair. Observations lasted maximally 10 min and an effort was made to obtain data from

each pair at least every five days. 15 pairs were protocolled from April 1979 to February 1980 and 22 pairs from February 1980 to July 1980. This resulted in over 1400 observational periods.

The same pairbond, courting and aggressive behaviors were recorded as during the flock protocols. In addition, a more sensitive measurement of aggressive behavior was possible as less intensive attacks of individuals could be counted. These attacks were defined as a threat with movement directed towards the opponent.

## II. Analysis of Behavioral Data

In order to compensate for variations in the number of geese observed and the duration of the flock protocols, a corrected value had to be determined for each behavior and each observational period. The number of geese present was multiplied by the minutes of observation, producing a value of goose-min for each protocol. Pairbond displays and aggressive behavior were then expressed as the occurrences per 1000 goose-min. Courting was treated differently because only the identity of geese and not the number of times they courted was recorded. The percentage of geese courting was calculated for each observational period.

The data were broken into categories according to the social status of the individual. As depicted in Fig. 1, the following social classifications were used:

1) juveniles from 7 to 22 months of age, when the first stable pairbonds are formed,
2) subadults from 22 to 34 months and
3) adults over 34 months of age.

Barheaded geese, like other *Anserini* (CRAMP and SIMMONS 1978), are capable of reproducing when they are two years old but are seldom if ever successful before they are three.

Data from individual protocols were treated as follows: Values for attacks and pair bond displays were expressed as occurrences per min. For courting, the % of protocols in which it occurred was calculated over the defined time units (see below). The adults here were broken down into two categories: successful and unsuccessful breeders or adults with and without goslings. Although the actual difference first occurred in May when the goslings hatched, the definitions were made retroactive to the onset of nesting. The classifications remained the same until the following March.

The beginning of the breeding season was spread out over a month in the Seewiesen population. As a result, it was necessary to standardize the individual data from adults with respect to the phase of reproduction to make them more cohesive. The phases were as follows:

*phase 1:* 4—2 weeks before the first egg was laid
*phase 2:* the two weeks before the first egg was laid
*phase 3:* egg laying
*phase 4:* the first two weeks of incubation

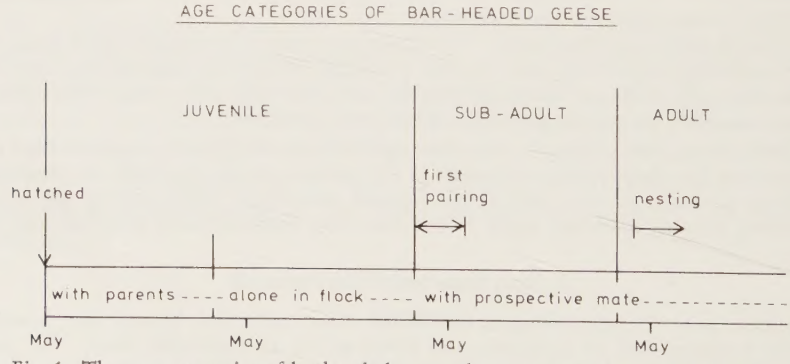



*Fig. 1:* The age categories of barheaded geese, the accompanying social situation and the occurrence of reproductive behavior. The first three years of life are represented

*phase 5:* the last two weeks of incubation
*phase 6:* the two weeks after the female had left the nest
*phase 7:* the period up to the primary molt
*phase 8:* the flightless period of the molt
*phase 9:* the remaining part of August

Data from other times of the year were presented on a monthly basis. In total, the year was broken down into 16 time units. Subadult goose information was put together on a monthly basis although irregular nesting activity occurred in this social class. Means were plotted in all the figures and when n exceeded 4, the standard error was indicated.

## III. Collection of Physiological Data

The data on weights and hormones were collected from geese caught in the feeding cages. Only those on incubation were obtained by capturing females on the nest. In total, over 600 plasma samples were collected from barheaded geese during the study. Most catches in the feeding cages occurred in the morning, however, a few geese were caught in the evening. Normally, catches totalled 2—4 geese, but on occasion, more geese were trapped at once (max. 15). The approximate time intervals involved were 5 min from closing the trap door to the first blood sample and then 3 min for each goose. The actual collection of blood took less than one min. An effort was made to get 2 ml of blood from each bird. Blood was taken from the leg vein with a disposable 5 ml syringe which had been prerinsed with a solution of heparin in 5000 IU/ml and $NaN_3$ 1 g/l in distilled water. The samples were then centrifuged at 4000 g for 15 min and the plasma was drawn off with a syringe. It was then frozen and stored at —25 °C until assayed. After having taken the blood samples, the geese were weighed and released immediately.

One unexpected problem arose during the study in regard to sample distribution over the year. The readiness of geese to enter the catching cages was seasonally dependent. For instance, it was difficult to catch geese from the second half of December to the middle of February. Also, just before and during the flightless period of the molt non-breeders and unsuccessful breeders were not caught easily, although successful breeders went into the cage readily. As a result, the number of plasma samples and therefore the physiological data were not equally distributed over the whole year.

## IV. Measurement of Hormones in Plasma

Hormonal titers were measured using previously developed radioimmunoassays (RIA) for various hormones. Proteohormones and thyroxine were measured directly in plasma. The steroids required an organic solvent extraction and in some cases chromatographic separation before assaying. The buffer system, standard, antiserum, plasma volume, sensitivity and inter-assay-variation in pools of goose blood for each hormone are listed in Table 2.

The following prerogatives were used as a basis for assay validation:
— plasma dilutions had to parallel those of the standard,
— a given amount of added hormone had to be recovered in the RIA,
— for pituitary hormones, pituitary extracts also had to parallel the standard.

All samples were assayed in duplicate and pools of goose plasma with known amounts of hormone were included in each assay. In steroid assays, blanks of ligand-free chicken plasma were also assayed. 125 I samples were counted either on a Beckman gamma 4000 or a Berthold Gammazint and 3H samples on a Berthold BF 8000. Theoretical aspects of RIA are described in Walker and Keane (1977).

The following hormones were measured:

### 1) Luteinizing Hormone LH

The RIA for LH developed by Follett, Cunningham and Scanes (1972) was used. A purified chicken LH (AE1) served as a standard and an anti-chicken LH (16/6) as an anti-

*Table 2:* Information on the radioimmunoassays

| Hormone | Standard | Label | Antisera and concentration | Buffer | Plasma | Sensitiv. pg / tube | 50 % B / F pg / tube | Interassay variation |
|---|---|---|---|---|---|---|---|---|
| LH | AE-1 Follett | 125 I AE 1 | 16/6 1:50,000 Follett | .5M PBS w / 1g / l BSA pH 7,05 | 20 µl | 4 - 240 | 20 | 11 % |
| Prolactin | NIAMDD Ovine PRL NIHPRLS 12 | 125 I NIHPRL S 12 | AGP-4 1:5000 McNielly | .5M PBS w / 20g / l BSA pH 7.4 | 40 µl | 40 - 4000 | 460 | - |
| T 4 | T-2501 Sigma | 125 I T4 NEX 11 H | Anti T4 1:6000 Merrett | see LH | 20 µl | 10 - 3000 | 80 | 10 % |
| DHT | A-8380 Sigma | 3 H - DHT NET 544 NEN | Anti Testo 550 / 3 1:2500 Spec. Antisera | .5M PBS w / 1g / l Gelatine | 200 µl | 15 - 500 | 130 | 15 % |
| Testo. | T-1500 Sigma | 3 H - T TRK 402 Amersham | Anti Testo 550 / 3 1:3500 Spec. Antisera | see DHT pH 7.2 | 200 µl | 6 - 600 | 70 | 8 % |
| Oestrad. E 2 | E 8875 Sigma | 3 H - E 2 TRK 322 Amersham | Anti E 2 1:20,000 Spec. Antisera | see DHT | 200 µl | 2 - 250 | 30 | - |
| Cortico-sterone | C 2505 Sigma | 3 H - Cort. TRK 406 Amersham | 110 / B 1:2000 Underwood | see DHT | 20 µl | 6 - 400 | 20 | 11 % |

serum. The validity of this assay has been tested in snow geese, *Anser caerulescens*, by CAMPBELL et al. (1978). They found no cross reaction between the antiserum and thyroid stimulating hormone (TSH).

### 2) I-Thyroxine T4

The system developed by HALL (1979) was used to measure T4. In contrast to most other RIA's for T4, this system does not use 8-anilino-1-naphthaline sulfonic acid (ANSA) to block non-specific binding due to plasma proteins which bind T4. Specific binding proteins with a high affinity for T4 have not been found in birds (HENIGER and NEWCOMER 1964; HALL 1979). Recently, a binding prealbumin was measured in quail (EL-SAYED et al. 1980) and found to have an annual cycle. The affinity of this binding albumin, if it occurs in geese, is probably not strong enough to interfere with the RIA.

### 3) Prolactin

A RIA for prolactin developed by MCNEILLY et al. (1978) was used. It is a heterologous system which utilizes a purified ovine prolactin (NIAMDD-OPRL NIH-P-S12) as a standard and an antiserum (AGP-4) raised in guinea pigs against human prolactin. The prolactin assay was only done on plasma samples from adult geese because of the limited amount of antiserum available.

### 4) Dihydrotestosterone DHT, Testosterone and 17-$\beta$ Oestradiol

These hormones were measured using partition chromatography coupled to RIA's as described by ABRAHAM (1973) and WINGFIELD and FARNER (1975). WINGFIELD's system I was used with slight modifications: After tracers of each hormone (2000 cpm) had been added to 200 µl samples of plasma and allowed to equilibrate for 3 h, the samples were extracted with 4 ml diethyl ether. The residues were taken up in 1.2 ml of ethyl acetate in iso-octane (2 %) and placed onto Celite (Johns Mannsville) micro columns for chromatography which had a 0.25 g water trap (Celite : water = 3 : 1) and a 0.75 g mobile phase (Celite : propylene glycol : ethylene glycol = 6 : 1.5 : 1.5; w : v : v).

Varying mixtures of ethyl acetate and iso-octane were used to separate the steroids dissolved in the stationary phase of the column. A 3 ml fraction of pure iso-octane removed

the lipids. DHT was then separated with a 10 % mixture of ethyl acetate in iso-octane (4.5 ml), testosterone with a 20 % mixture (4.5 ml) and 17-$\beta$ oestradiol with a 40 % mixture (4.5 ml).

The samples were dried after chromatography, taken up in 200 $\mu$l of ethanol and dried again. 200 $\mu$l of buffer was then added and the samples were allowed to sit over night. 50 $\mu$l were used to determine the % of recovery and two 50 $\mu$l aliquots went into the RIA. The assays were performed in 11 × 70 mm plastic test tubes. After adding antiserum and label, the tubes were allowed to incubate 48 h at 4 °C before separation. Acid washed charcoal in buffer (1 g/l) was used to separate the bound and unbound fractions.

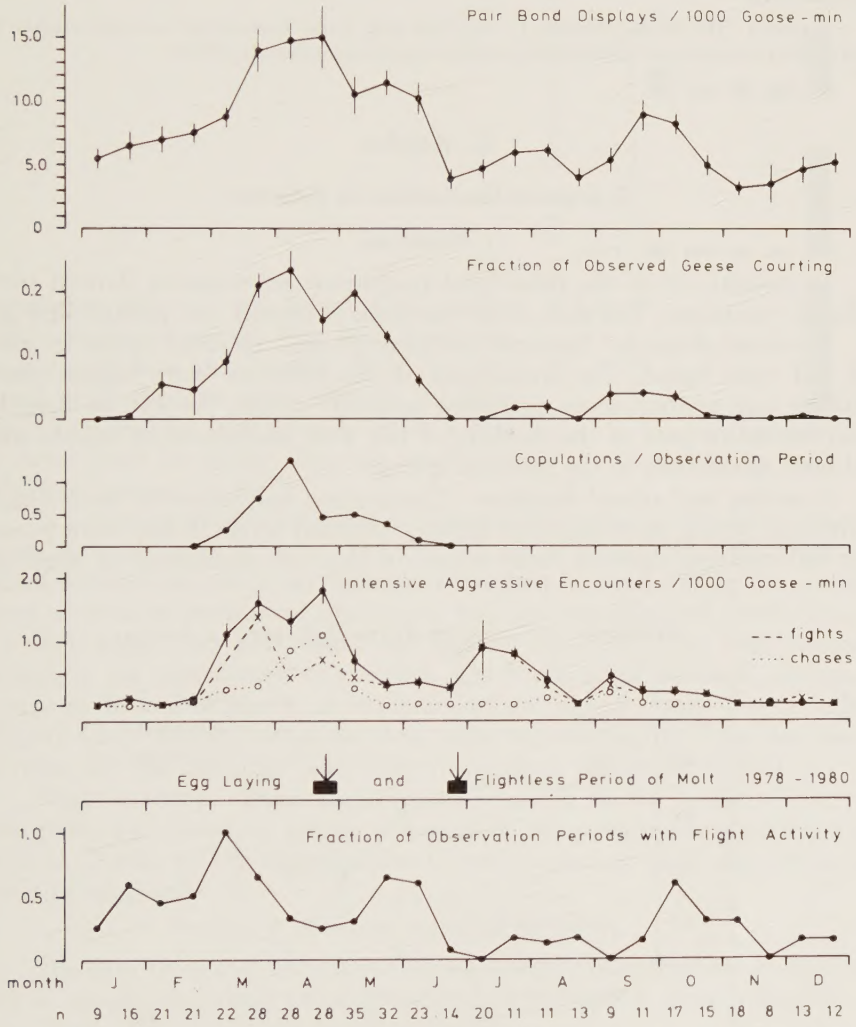



*Fig. 2:* Data on seasonal changes in the frequencies of behavior in the entire flock calculated from flock protocols. n is the number of protocols per two week interval. Means with SE's are plotted. The onset of egg laying and molting dates are included. Solid bars represent the quartiles and arrows the median dates

#### 5) Corticosterone

This hormone was measured in 20 $\mu$l of plasma, after extraction with 3 ml diethyl ether, using an antiserum developed by UNDERWOOD and WILLIAMS (1972). The same procedure was used in the assay as described above for the other steroids, except that the extracted plasma was redissolved in buffer without chromatography.

The data on hormones were organized into the same phases as the behavioral data from individual protocols. In many cases, the levels of hormones in plasma were below the detectable limit of the RIA. The lowest detectable amount was assigned to these samples instead of defining their hormonal titers as being equal to zero. As a result, the baseline levels in the annual curves were in part defined by the assay's sensitivity and may have been lower than indicated.

Statistics: The Mann-Whitney U test, sign test, linear correlation test and median test were used to compare sets of data for statistical significance (SIEGEL 1956).

## C. Results

### I. Seasonal Fluctuations in Behavior

#### 1. Flock Data

In general, all of the behavioral parameters investigated showed strong seasonal variations. The data from the flock protocols are plotted in Fig. 2.

*Pairbond displays:* Seasonal fluctuations with elevated levels in spring and fall were found. The frequencies of this behavior were highest during breeding and periods when migration normally occurs. As will be described later, the major part of the displays in fall were performed by adults which had bred successfully in the previous spring.

*Courting and sexual behavior:* Copulations only occurred in spring. In courting, a spring maximum and slightly elevated levels in fall were present. The fall courting differed from spring in that no copulatory or even pre-

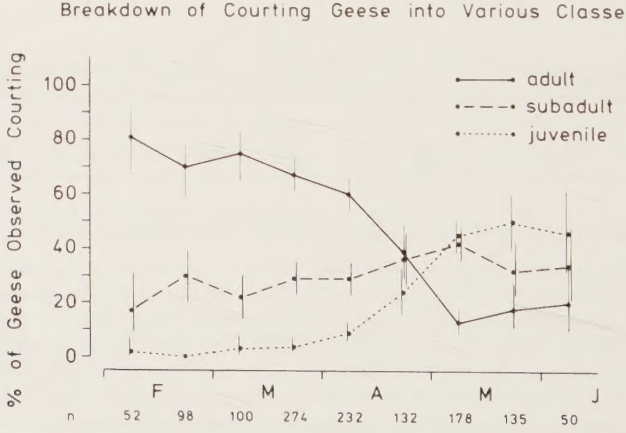



*Fig. 3:* A breakdown of the courting data during the breeding season from Fig. 2 into age categories. n is the sum of individuals seen courting over the two week intervals. The percentage of n per age class is plotted with the confidence intervals

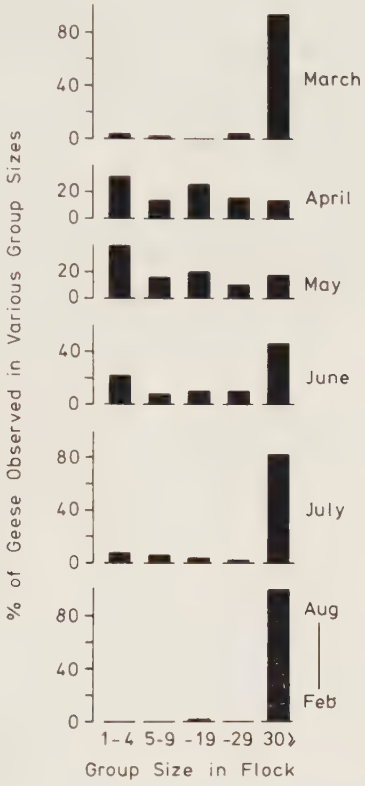



*Fig. 4:* The distribution of geese in terms of group size, calculated on a monthly basis. The data resulted from counts done at the beginning of each flock protocol

copulatory behavior was found. Only angle-neck courting occurred. The mid April dip in courting had two causes. First, in late April many females were already incubating, and secondly, the juvenile geese began to court later in spring than the adults or subadults, as seen in Fig. 3.

*Intensive aggressive encounters:* There were peaks in aggressive behavior in spring and again in July. The breakdown of these data into fights and chases showed that the latter were most frequent in April during the establishment of nesting territories, egg laying and the beginning of incubation. On the other hand, two peak values for fighting occurred. They were related to changes in the cohesiveness of the flock. The break-up of the flock into smaller groups at the end of March corresponded to the highest frequencies of fighting (Fig. 4). Later, in July, when the flock came together again, there was another increase. At this time, the rank order in the flock was re-established.

*Flight activity:* Three major peaks occurred in the course of the year. One peak was found in spring, a second in the post-breeding period and a third in October. They corresponded to periods during which free-living conspecifics migrate.

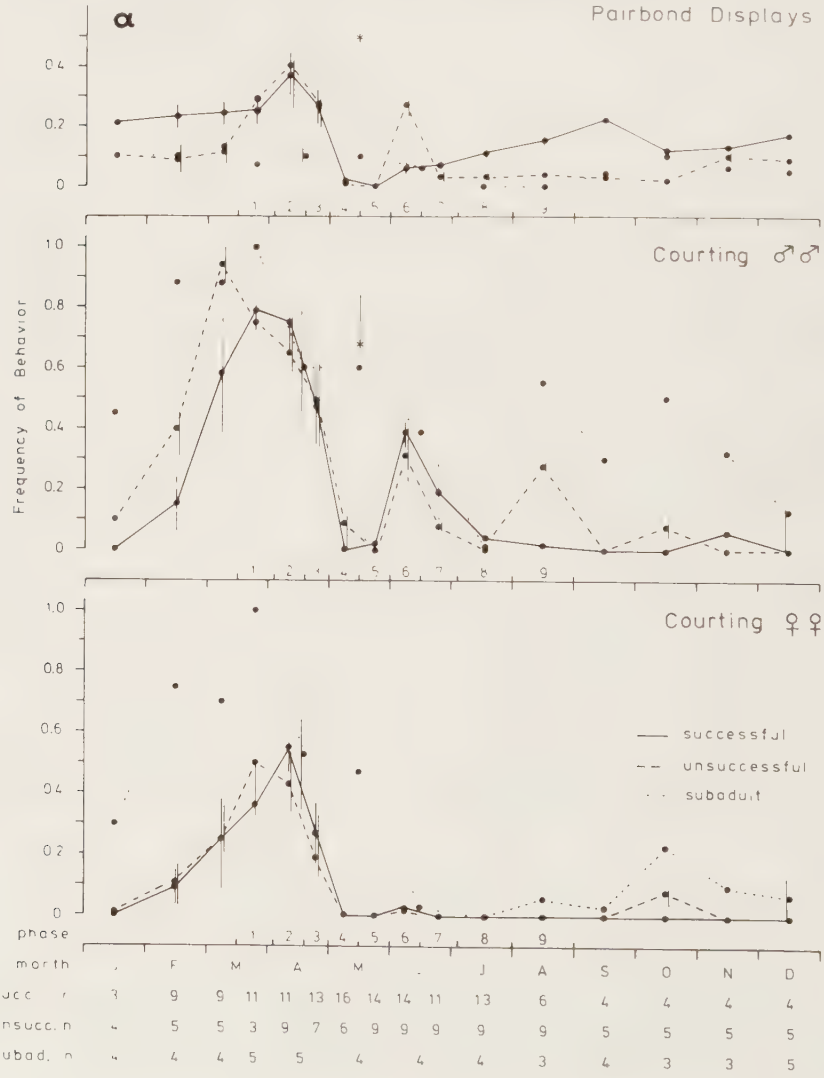
### 2. Data from Individual Protocols

The data from each individual were averaged for each phase of reproduction or month, and these values were used to compute a mean value for each social class. The results are shown in Fig. 5.

*Pairbond displays:* As seen in Fig. 5, the successful and unsuccessful breeders had similar values in pairbond displays from the first phase of reproduction through incubation (phases 1 to 5). There was a large decrease during

incubation (phases 4 and 5). When the female came off the nest for pauses, however, the frequency went up to pre-incubational values. The data from nest pauses are indicated by asterisks on the diagram. When the female abandoned the nest (phase 6), the unsuccessful breeders had significantly higher levels than adults leading young ($p < .001$). This had reversed by the

*Fig. 5:* Data on the seasonal changes in the frequency of behavior in geese of various social classes, calculated from individual protocols. Pairbond displays and attacks are plotted on an occurrence/min basis. Courting values are the fractions of observational periods in which courting or sexual behavior occurred. Means with SE's in $n \geq 5$ are plotted. Each point is the average of the means of individuals. n's are the same in both diagrams. Asterisks indicate values from data collected during female nest pauses



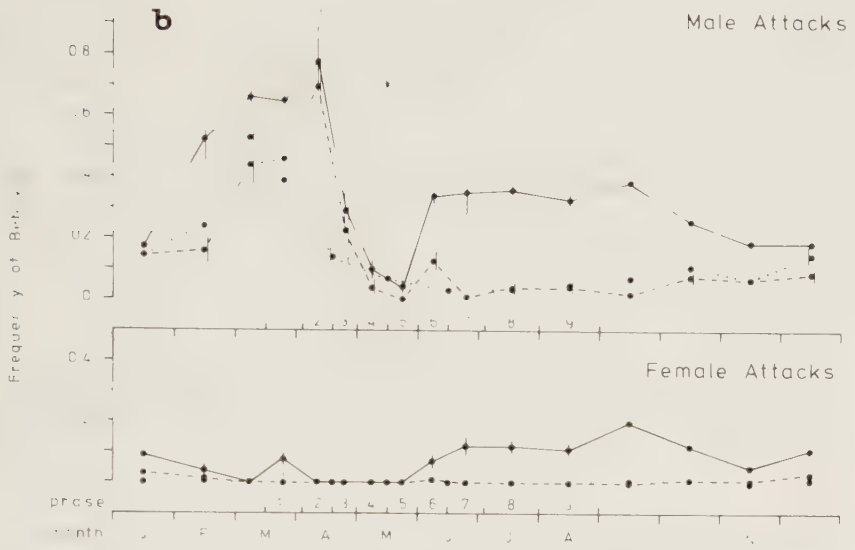



*Fig. 5*

flightless period of the molt (phase 8) and remained so until the following spring. The successful breeders had significantly higher levels ($p < .001$) during this period. Recently paired subadults did not perform pairbond displays frequently. The first real increase took place the following spring when they became adult.

*Courting:* Differences in the amount of courting were found between social classes. Subadults courted consistently more than adults (Fig. 5 a). These differences were especially pronounced in males. Values for subadults during September, October and November were significantly higher than the values of adults ($p < .05$). Successful and unsuccessful breeders were similar except in February and the first half of March of the following year, when unsuccessful individuals tended to court more although not significantly.

*Aggressive encounters:* The data on attacks are plotted in Fig. 5 b. For both successfully and unsuccessfully breeding males, the peak of aggression was 2—4 weeks before the first egg was laid (phase 2). Males established nesting territories at this time. Outside of the nesting season, there were clear differences between social classes in the amount of aggressive behavior. Successfully breeding males and females had significantly higher levels ($p < .001$) from the time the female and goslings had left the nest (phase 6) through September. The differences decreased from October to January but were again evident in male attacks during February and March of the following year.

## II. Physiological Results on the Flock

### 1. Egg Laying Dates

The median and quartiles of the egg laying from 1978 to 1980 are shown in Fig. 2. Timing was remarkably constant over the three breeding seasons

(Table 3). The slightly later dates in 1979 and 1980 were a reflection of the increased number of subadults in the flock from 1978 to 1980 (Table 1). Subadults and three year old geese laid later than adults. Their median onset of egg laying was April 29.

*Table 3:* Egg laying (median dates with quartiles)

| | | | |
|---|---|---|---|
| 1978 | 18. 4. | 15. 4. / 25. 4. | n = 124 |
| 1979 | 20. 4. | 17. 4. / 29. 4. | n = 161 |
| 1980 | 21. 4. | 17. 4. / 28. 4. | n = 178 |

### 2. Primary Molt

Data on the onset of molt are presented in Table 4. In general, successful breeders molted earlier than unsuccessful breeders although the differences were not statistically significant. Juveniles molted with or after the unsuccessful breeders. The subadults molted ten days earlier in 1979 than in 1980.

*Table 4:* The onset of primary molt (median dates with quartiles)

| | | | | |
|---|---|---|---|---|
| 1979 | suc. breeders | 20. 6. | 17. 6. / 21. 6. | n = 18 |
| | uns. breeders | 26. 6. | 23. 6. / 1. 7. | n = 22 |
| | subadults | 19. 6. | 17. 6. / 20. 6. | n = 15 |
| | juveniles | 1. 7. | 20. 6. / 7. 7. | n = 21 |
| 1980 | suc. breeders | 20. 6. | 17. 6. / 25. 6. | n = 23 |
| | uns. breeders | 29. 6. | 25. 6. / 29. 6. | n = 13 |
| | subadults | 29. 6. | 25. 6. / 29. 6. | n = 7 |
| | juveniles | 29. 6. | 29. 6. / 29. 6. | n = 12 |

The onset of the molt was examined to determine whether having goslings affected the timing of the molt. Data in Table 5 show that the interval between the females' leaving the nest and the onset of the molt was similar in geese with and without goslings. As can be deducted from the differences in their molting dates (Table 4), the unsuccessfully breeding females incubated a few days longer and therefore left the nest later (26. 5.; 20. 5./29. 5.; median with quartiles) than successful females (22. 5.; 17. 5./22. 5.). Individual variation in the timing of egg laying, incubation and molt over the three year study period was small (Table 6). Even in cases where a change in breeding

*Table 5:* The interval between the onset of molt and abandoning the nest (mean and SE over three years of observation)

| | males | females | |
|---|---|---|---|
| successful breeders | 30 days ± 1 | 30 days ± 1 | n = 20 / 21 |
| unsuccessful breeders | 31 days ± 1 | 33 days ± 1 | n = 17 / 18 |

*Table 6:* The mean variation in individuals (mean and SE over three years of observation)

| | | |
|---|---|---|
| Egg laying | 5 days ± 1 | n = 16 |
| Incubation | 4 days ± 1 | n = 17 |
| Molt | 4 days ± 3 | n = 23 |

success occurred, the mean variation in the onset of molt did not exceed four days (n = 14).

### 3. Weights

The weights of both adult males and females fluctuated seasonally (Fig. 6). They increased in fall, leveled off in December and decreased in February. The amount of annual variation in males, expressed as the percent of maximum weight, was 23% and in females 28%. The percentage differences between males and females were due to the females' storing up necessary reserves for egg laying and incubation. After decreases during incubation, the females continued to gain weight into the molt. No differences were found between females with or without goslings. In males, there was a tendency for successfully breeding individuals to weigh more than the unsuccessful ones, although the differences were not statistically significant. The means of successful males were higher in 12 of the 16 time periods.

## III. Plasma Titers of Hormones

The data have been grouped together according to age categories and sex. Adult male data are shown in Fig. 7, adult female data in Fig. 8. The results of subadult and juvenile geese have been plotted together in Fig. 9 for the males and in Fig. 10 for the females.

### 1. Luteinizing Hormone LH

Seasonal changes in LH were found in both sexes of all social classes. There were high values in spring, extremely low values in summer and then slightly elevated levels in fall. The peak values in males occurred in phase 2, just prior to the female's egg laying. At this time, both sexual and aggressive behavior were at a maximum. The females' peak values occurred during egg laying (phase 3).

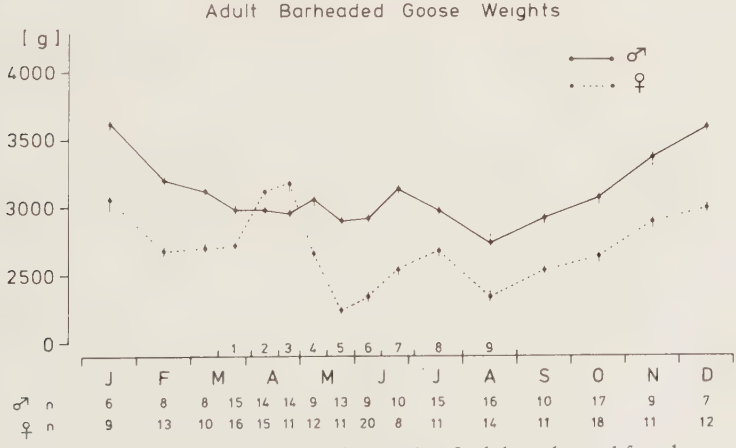
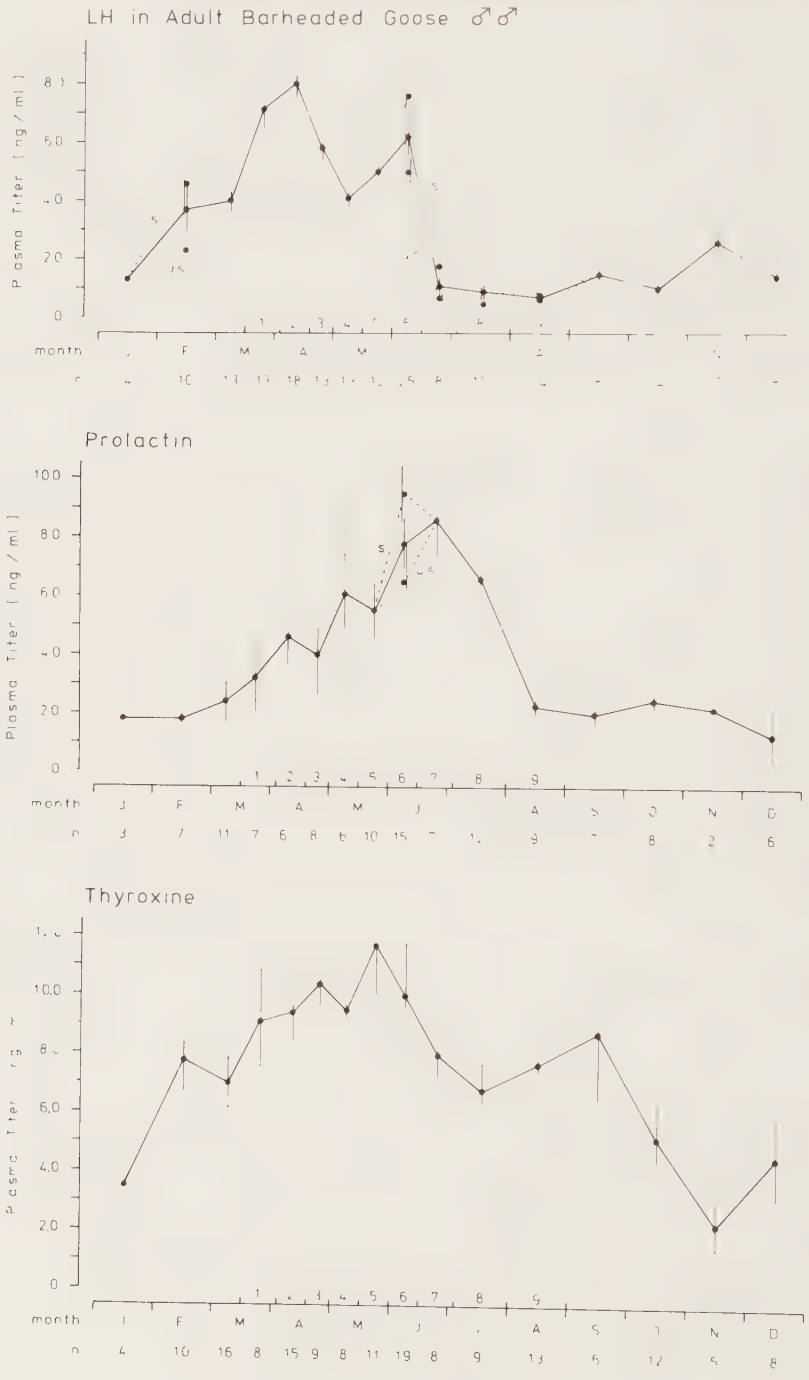



*Fig. 6:* Annual fluctuations in the weight of adult males and females. Means with SE's are plotted

*Fig. 7:* Annual fluctuations in the plasma titers of various hormones in adult males. Means with SE's, if n $\geq 5$, are plotted. Differences between successful (s) and unsuccessful (us) breeders are plotted when they occurred



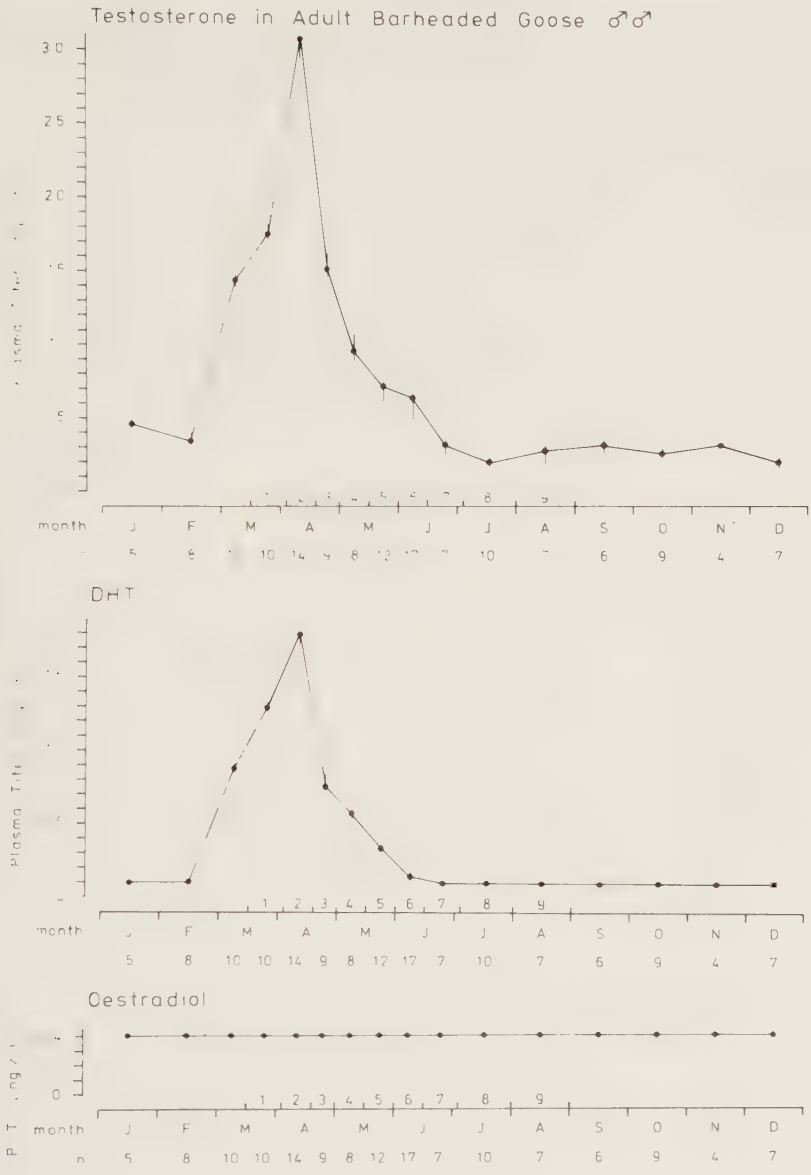
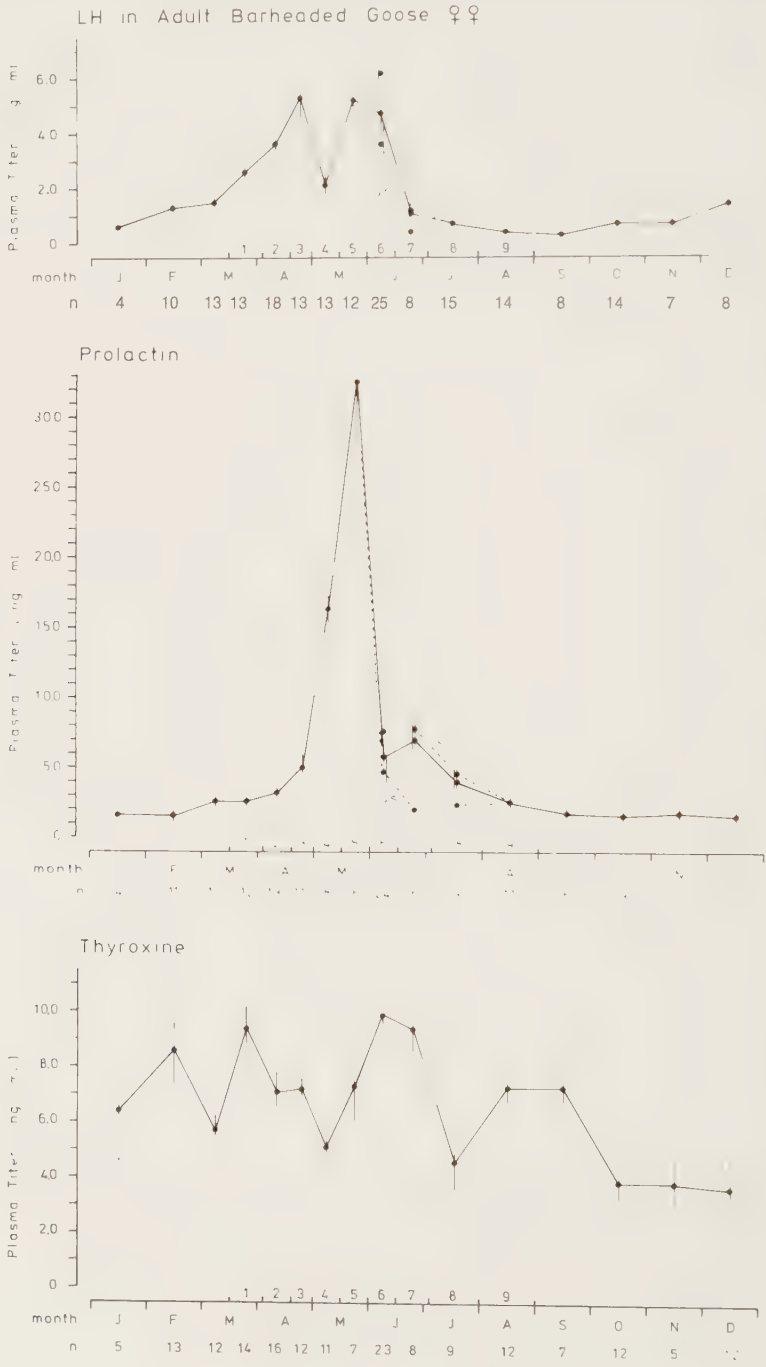



*Fig. 7*

Both male and female adults showed LH decreases during incubation. LH titers of females rose, however, significantly in the second half of incubation ($p < .01$). After incubation (phase 6), a significant increase ($p < .05$) was found in successfully breeding males while LH plasma concentrations in unsuccessful males did not change. Successfully breeding females had significantly higher levels of LH than unsuccessful ones ($p < .05$) after incubation.

*Fig. 8:* Annual fluctuations in the plasma titers of various hormones in adult females. Means with SE's, if n $\geq 5$, are plotted. Differences between successful (s) and unsuccessful (us) breeders are plotted when they occurred



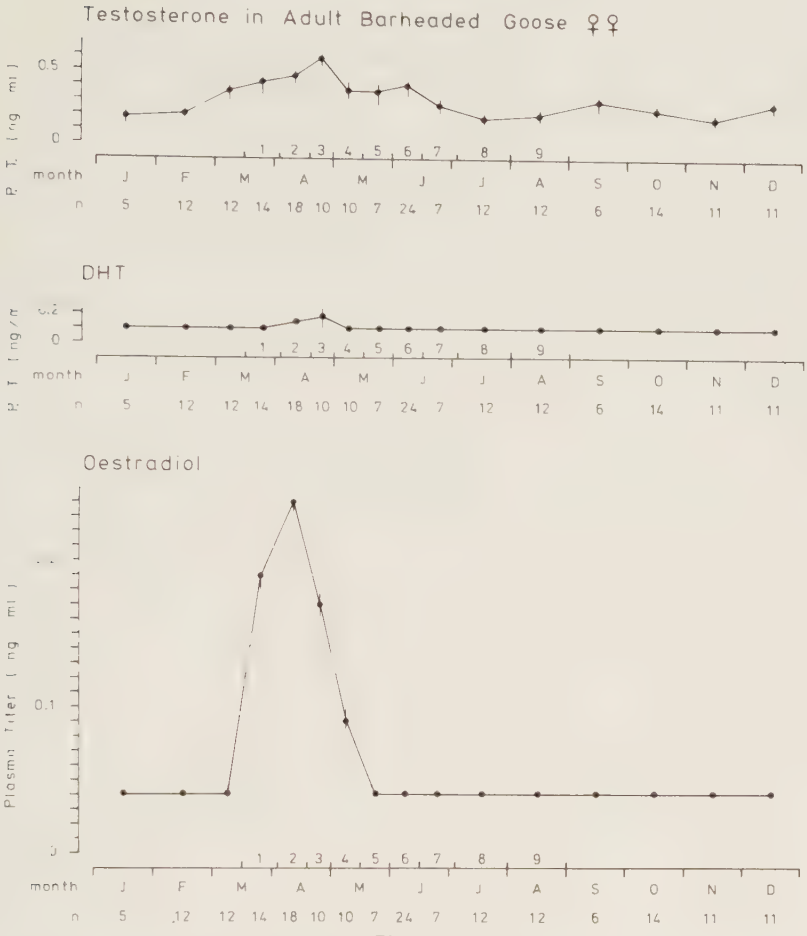



*Fig. 8*

There were also differences between the two male groups in February prior to the next reproductive period ($p < .05$).

Subadult geese showed the same seasonal patterns in LH as adults. Nesting activity in this group was restricted to nest building, egg laying and short bouts of incubation. So, the forementioned decreases and increases were not pronounced.

Juvenile males showed delayed peaks in LH relative to the adults and subadults. Juvenile females had only slight increases in LH during their second spring and fall. This is in line with the observation that juvenile females neither laid eggs nor showed nesting behavior.

### 2. Prolactin

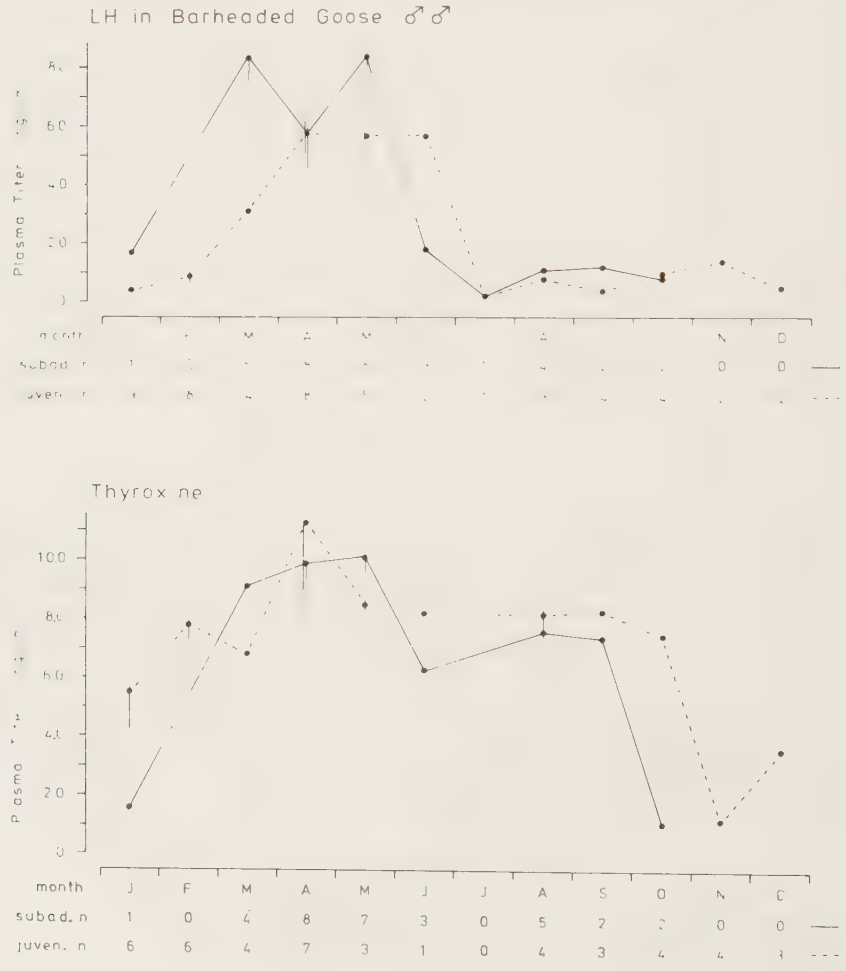
The prolactin assay was only done on plasma samples from adult geese because of the limited amount of antiserum available.

The seasonal trends in prolactin were different for males and females. Female prolactin titers were highest during incubation (phase 4 and 5) and in the males, they were elevated from the end of incubation through the primary molt (phases 6, 7 and 8).

Successfully breeding females brooded their goslings after leaving the nest. Their levels of prolactin declined less than those of females without goslings ($p < .01$). Brooding behavior ceased with the onset of the primary molt (phase 8), and the prolactin levels dropped concomitantly.

Plasma decreases in LH found at the beginning of incubation (phase 4) were checked with regard to their relationship to prolactin increases. The individual levels of LH in males and females showed no significant negative correlation with their levels of prolactin ($r = -.11$ for males and $r = -.35$ for females).

*Fig. 9:* Annual fluctuations in the plasma titers of various hormones in juvenile (- - - - -) and subadult (———) males. Means with SE's, if $n \geq 5$, are plotted



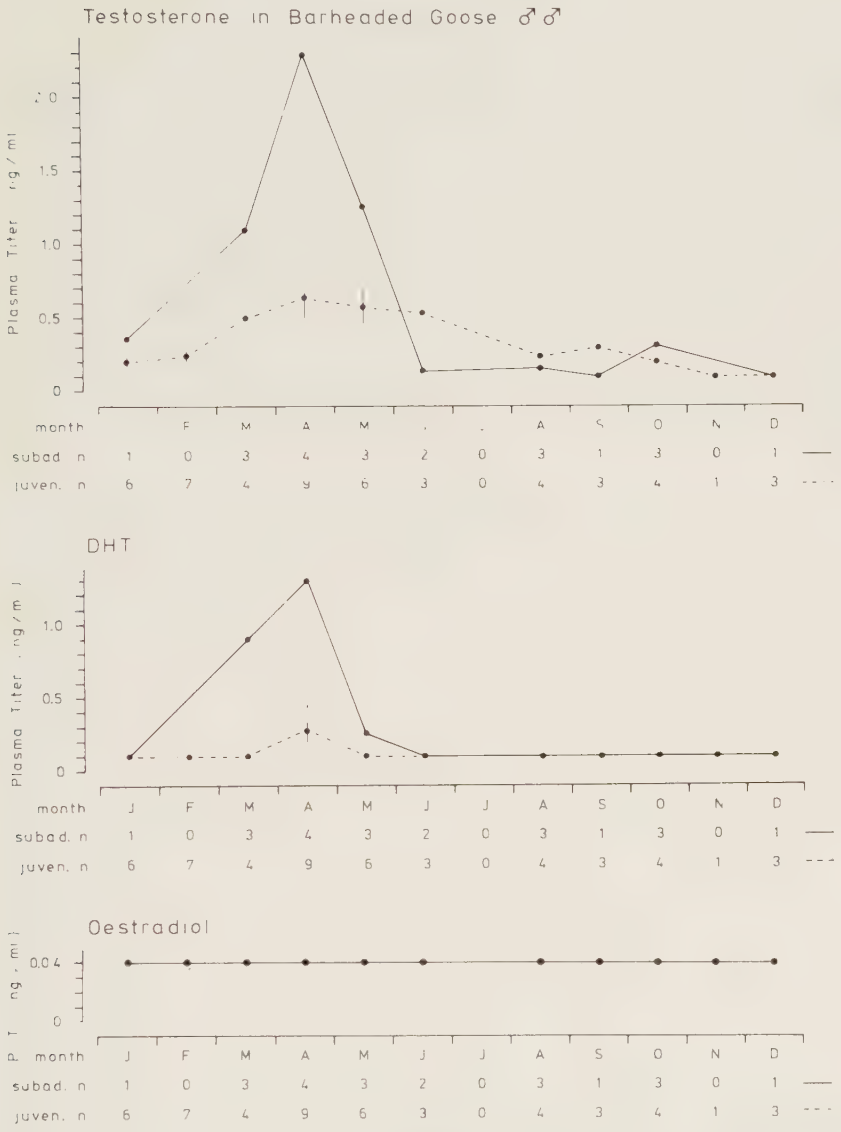



*Fig. 9*

### 3. Thyroxine T4

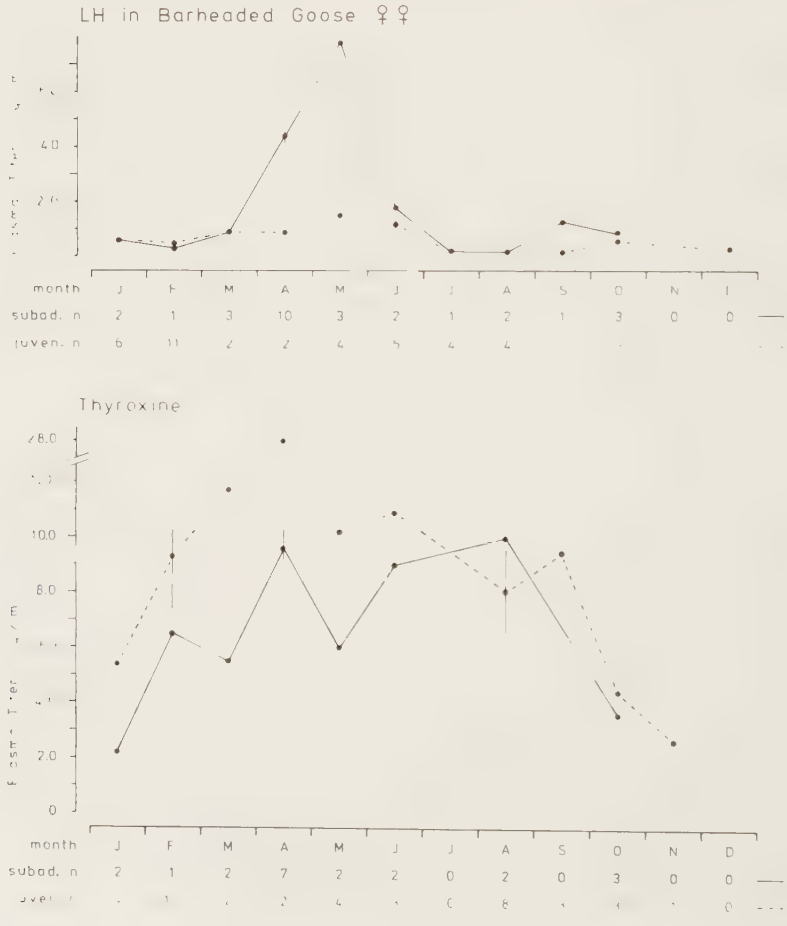
In thyroxine, the seasonal patterns were not clear. The only consistent tendency was that the plasma titers were high in spring and summer, and low in late fall. For adult females, the curve was more irregular than that for adult males as plasma titer decreases were quite pronounced in early March, during incubation (phase 4) and the molt (phase 8).

#### 4. Testosterone

In adult males, testosterone showed a strong annual cycle. Plasma levels increased in March, reached a maximum in the two weeks before egg laying (phase 2), simultaneously with LH, and decreased throughout the nesting period to a minimum during the molt. Autumnal increases were only found in a few individuals. The data on subadult males were very similar to those of the adults. Juvenile males, on the other hand, had smaller increases in testosterone than the adults and their levels remained elevated longer.

The patterns of testosterone in adult and subadult females were similar to those in males. However, the plasma titers were generally much lower than in males. Seasonal changes were also less pronounced. Peak values occurred during egg laying (phase 3), simultaneously with the peaks in LH. Juvenile females had no spring increases in testosterone but tended to have slightly elevated levels in autumn.

*Fig. 10:* Annual fluctuations in the plasma titers of various hormones in juvenile (- - - - -) and subadult (———) females. Means with SE's, if n ≥ 5, are plotted



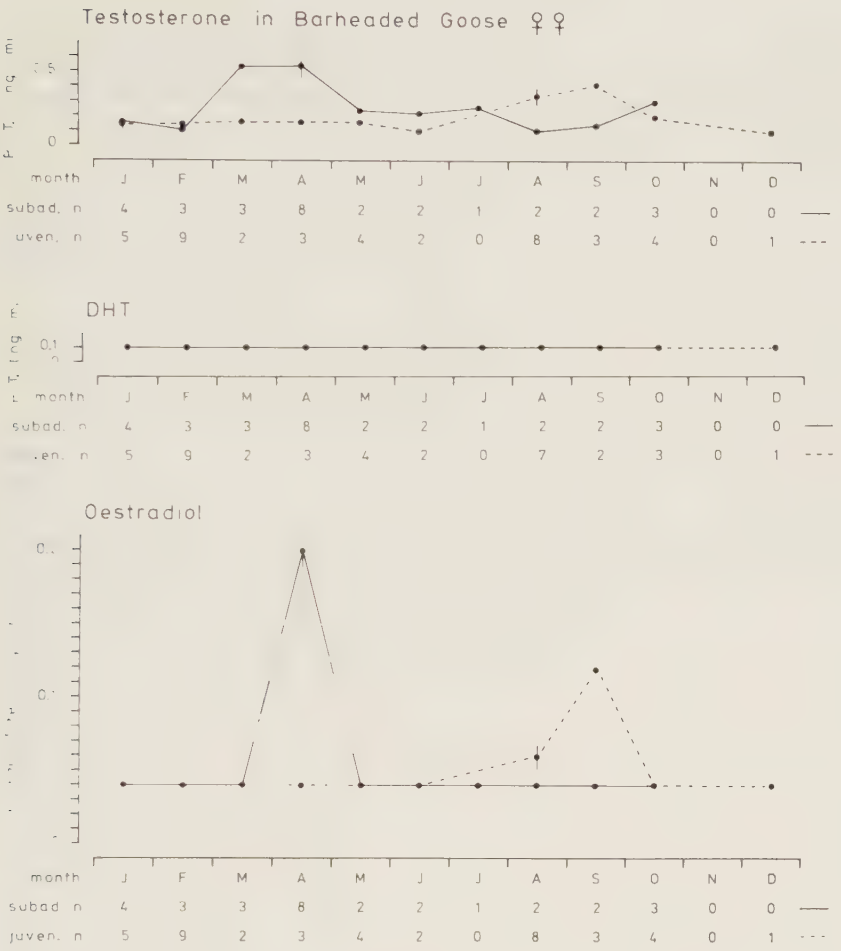



*Fig. 10*

The differences between the values of successful and unsuccessful breeders were not distinct. For males, they were only significant when the data were pooled from August through November ($p < .05$). After leaving the nest (phase 6), the unsuccessfully breeding females showed slightly higher levels than the successful ones ($p < .05$).

A comparison of testosterone levels with prolactin and LH in adult males during the breeding season was done. There was a correlation between individual concentrations of testosterone and LH ($r = .62$; $p < .01$) during periods where both hormones increased (March and phases 1 and 2). No significant negative correlation was found between individual concentrations of testosterone and prolactin ($r = -.22$) during periods when testosterone decreased (phases 3, 4 and 5).

### 5. Dihydrotestosterone DHT

DHT in adult and subadult males paralleled testosterone in spring and was not present in measurable amounts at other times of the year. There were no quantifiable changes in the plasma DHT levels of females.

### 6. 17-$\beta$ Oestradiol

No oestradiol was found in the males, whereas in the females a marked seasonal pattern existed. Peaks for adult and subadult females occurred in spring. From the data of adult females it is evident that the peak occurred just prior to egg laying (phase 2). A significant, positive correlation was found between individual concentrations of LH and oestradiol during periods of increase in the latter ($r = .51$; $p < .01$, in phases 1 and 2). Juvenile females had elevated levels in August and September of their second year.

### 7. Corticosterone

The levels of corticosterone were determined but the resulting annual curves were so irregular that the data were not presented in the report. A further examination of the data showed a dependency between the position in the order of being caught and the plasma titer of corticosterone (Fig. 11). In both adult males and females, the levels of corticosterone were already elevated in the first goose sampled. The means peaked by the time the third goose was caught or at about 14 min after capture (see Methods). The data

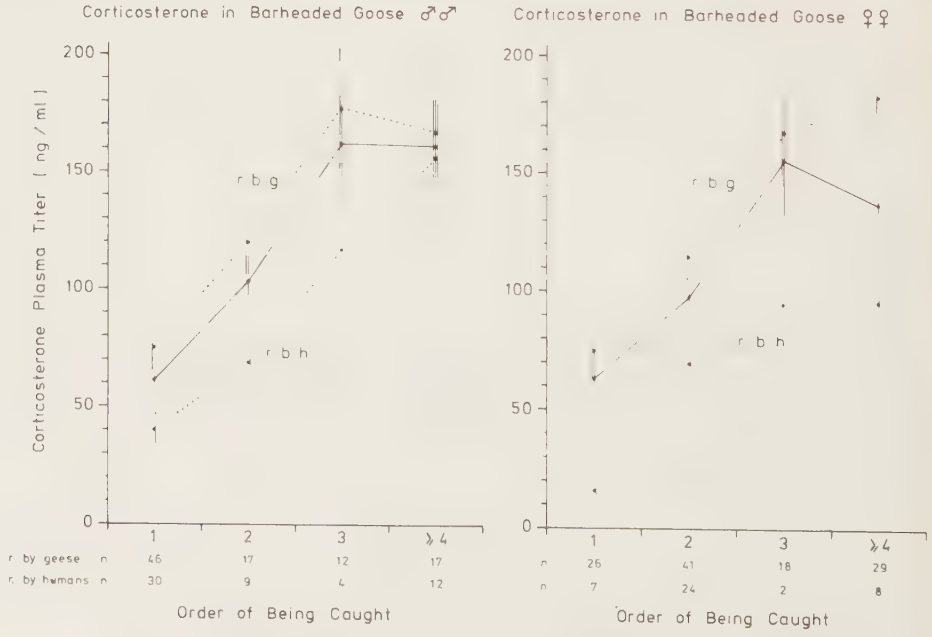



*Fig. 11:* Plasma titers in corticosterone, plotted in terms of the sequence being caught. The overall mean (solid line) has been broken down into the mean from birds raised by humans (r.b.h.) and those raised by geese (r.b.g.). Means with SE's are plotted

were broken down into samples from tame and untamed geese or geese which had been raised by humans and geese raised by goose parents. The results demonstrated that corticosterone increases in tame geese occurred more slowly than in untamed, and that in the females the levels of the tame geese did not even approach those of the untamed ones. The two categories were significantly different in both males and females in catching position 1 ($p < 0.01$) and position 2 ($p < 0.05$). The females also differed significantly in position 4 ($p < 0.05$).

## D. Discussion

The primary objective in this study was to collect detailed information on endocrinological and behavioral changes in a species. The results make it possible to examine whether certain hormones are correlated with an animal's tendency to behave in a certain way and whether or not that propensity was related to peripheral hormonal concentrations. To do this, it was important that the animals were tested in a natural environment going through a normal reproductive cycle as these criteria contain releasing factors and mechanisms which affect the frequencies of behaviors.

### Behavioral Data

The compiling of flock data enabled a comparison of the barheaded goose colony observed with free living geese. A number of results indicated that the population behaved normally. Egg laying and molting dates corresponded to those given for free living barheaded geese in the lower Hymalayas (Schäfer 1938; Dementiev and Gladkov 1967) and did not change substantially over the three year study. This regularity is a phenomenon known for other goose species (Murton and Kear 1973, 1976; Davies et al. 1969). The maturation processes were unaffected in the population in Seewiesen as geese first bred successfully when they were three years old. Subadults and three year old geese had later dates for egg laying as have been reported for wild goose populations (Raveling 1978; Finney and Cook 1978; Vermeer and Davies 1978).

Adult body weights showed fluctuations similar to those which have been found in wild populations despite the unrestricted feeding. The 23 % and 28 % annual variations in weight for male and female barheaded geese are comparable to Raveling (1979), who reported 21 % and 31 % variations for male and female Canada geese, *Branta canadensis*. Weight gains in late fall like those found here have been reported by Hanson (1962) and Raveling (1968) for Canada geese, and Matthews and Campbell (1969) for greylag geese. Although the geese did not migrate, they did evince a form of migratory restlessness in their flight activity. Increased flight activity occurred at times when free living conspecifics migrate (Kydyraliew 1967; Ali 1979). Post incubational flight activity was reminiscent of the molt migration, which has been described for other goose species (Salomonsen 1971).

In effect, the population here showed seasonally linked behaviors similar to those in populations of wild geese.

In this report, the data on individual geese have been utilized to investigate the effects of age and social status on annual cycles in behavior and hormones. The behavioral results showed that juvenile males courted later in the year than adult males. Juvenile females rarely courted. After pairing as subadults, courting was much more intensive. It continued into late fall and increased again in January, while little or no courting activity was present in the adults. The maxim stated by LORENZ (1959) that courting and sexual activity precede triumph ceremonies in the development of pairbonds in geese is reflected in the data of the subadults. The frequency of pairbond displays remained low throughout the entire spring and summer.

In adults, differences in the seasonal patterns of pairbond displays and aggressive behavior were found between successful breeders with goslings and unsuccessful breeders. The frequencies of attacks and pairbond displays during the summer and early fall were higher in both successful males and females than in unsuccessful ones. One reason for this was that the successful breeders defended feeding territories for their young. Dominance relationships might have also played a role. As is known for other goose species, adults with goslings have been found to be higher ranking than unsuccessful breeders, subadults and juveniles (HANSON 1953; BOYD 1953; RAVELING 1970; LAZARUS and INGLIS 1978). These authors all reported rank to be a function of family size and that the rank order was most frequently expressed in feeding situations. RAVELING (1970) also noted that the frequency of encounters was significantly higher in large families of Canada geese than in small families, pairs or single geese.

### Endocrinological Data

The endocrinological data have to be treated from both a physiological and behavioral standpoint.

*Luteinizing hormone* (LH) showed annual curves with high levels in spring and slightly elevated levels in fall which were in general agreement with the existing data on seasonal changes in other bird species (see FARNER and FOLLETT 1979 for a review; LINCOLN et al. 1980; SCHWABL et al. 1981).

The peak values in adult males occurred just prior to nesting, simultaneously with the peak of gonadal activity. Adult females had their highest values for LH later than the males, during egg laying, in agreement with results which have been reported for mallards, *Anas platyrhynchos* (DONHAM et al. 1976; GOLDSMITH and WILLIAMS 1980). The peak was probably associated with ovulation as is known from chickens (i.e. ETCHES and CUNNINGHAM 1977; JOHNSON and VAN TIENHOVEN 1980). At the beginning of incubation, LH levels in the geese dropped in both sexes, a phenomenon found in a number of bird species (COGGER et al. 1979; WINGFIELD and FARNER 1978 a and b; CAMPBELL et al. 1978; GOLDSMITH and WILLIAMS 1980; DONHAM 1979). LH levels in males and females increased again in the second half of incubation. The increases continued in successful breeders after incubation had

ended. Barheaded geese differ from other species studied up to now in that the second rise in LH was not directly associated with a reproductive effort. The only situations where marked LH increases after incubation have been known to occur are when re-nesting attempts ensued in Mallards (Donham et al. 1976), white-crowned sparrows, *Zonotrichia leucophrys* (Wingfield and Farner 1978 a, 1979) and ring doves, *Streptopelia risoria* (Cheng and Follett 1976; Silver et al. 1980). The relationship between this second peak and other hormones and its behavioral significance will be discussed below. LH levels in all classes had decreased before the onset of the molt. Elevated levels in some individuals were found again in fall.

Subadult males and females had similar patterns for LH except that decreases during incubation like those seen in adults were not pronounced. Subadult females only incubated for short periods. The lack of both extended incubation periods and LH decreases in subadult males and females infers that the decreases in adults were directly related to the females' sitting on the nest.

For juvenile males, the peak in LH was later than those for adults and subadults, and for juvenile females no substantial increases in LH were found at all. These differences were probably related to the presence of deferred maturity as has been described in Herring gulls, *Larus argentatus* (Scanes et al. 1974). There, spring peaks in LH and sexual maturity did not occur until the fourth or fifth year of life. However, high plasma titers were always found in fall. The situation in geese is different in that the immature phase is shorter. Partial testicular development takes place in juvenile male geese in their second spring, and in their third spring, as subadults, spermatogenesis occurs. In female geese, follicules do not develop until the birds are subadults (unpubl. data). In both juvenile Herring gulls and geese, the patterns of LH reflect then the process of developing sexual maturity, but show differences which are perhaps related to the species or the period of deferred maturity.

The relationship between LH, testosterone and oestradiol is of interest with regard to their seasonal fluctuations. Maung and Follett (1978), and Paulke and Haase (1978) have shown that peripheral androgens are probably under the control of LH. The coincidences of peaks for LH, testosterone and DHT found in this study support this assumption. During androgen increases in spring, a positive correlation was found between the peripheral levels of LH and testosterone. The correlation was not found later in the year. LH had a second peak which was not accompanied by testosterone increases. This suggests that there was some mechanism which modified the sensitivity of androgen-producing Leydig cells to LH. The result was that testosterone levels decreased while LH levels remained elevated (e.g. Wingfield and Farner 1978 b). The relationship between LH and oestrogen in females seemed to parallel that between LH and testosterone in males as a positive correlation existed between LH and oestradiol during periods of oestradiol increase. Unfortunately, little is known about the control of steroid genesis in the female.

Another aspect of the relationship between LH and steroids is the proposed existence of negative steroid feedback on the release of LH from the pituitary (see FARNER and FOLLETT 1979 for a review). The feedback is supposed to be an integral component in the annual gonadal cycle, as shutting off gonadotropin release causes regression of the gonads. The long period of elevated LH levels in barheaded geese is inconsistent with this hypothesis. Still, it is interesting to note that in both males and females, the second increase in LH levels occurred after testosterone levels in the males and oestrogen levels in the females had decreased. A hypothetical explanation for this situation might be as follows: LH stimulates gonadal growth and steroid genesis; increasing steroid levels then depress the release of gonadotropin to a point where the gonads regress but LH secretion is not shut off. In the absence of steroid feedback, LH levels increase again and later decrease as photo-refractoriness sets in. STOKKAN and SHARP (1980) have results in ptarmigans which are relevant to this hypothesis. Testosterone implants suppressed the production of LH in photoperiodically stimulated birds. Removal of the implants caused LH to increase and to complete the rest of the LH cycle, like in control animals which had been castrated but did not receive testosterone implants. The length of the cycle was dependent on when the implant was removed, and limited by the onset of the photo-refractoriness. LH decreases during the breeding season in geese were attributed to effects of incubation earlier in this discussion. The two proposals could be united by attributing an antigonadal or anti-androgen effect to incubation which causes a premature gonadal regression.

From a behavioral standpoint, the peak of LH in adult males occurred simultaneously with their peaks in aggressive and sexual behaviors during the two weeks before the females laid their eggs, as has been shown for ring doves (CHENG and FOLLETT 1976; SILVER et al. 1980), rooks, *Corvus frugilegus* (LINCOLN et al. 1980) and white-crowned sparrows (WINGFIELD and FARNER 1977, 1978a, b). The period after incubation, where the second peak of LH occurred, was marked by courting behavior and occasional copulations which never resulted in a second brood. Pairbonds in the geese remained intact after the breeding season. In white-crowned sparrows and mallards (see above), where detailed data on annual changes in LH are available, the pairbonds dissolved after the breeding season and neither high levels in LH nor sexual activity was found. It is of interest that in rooks there appeared to be a slight increase in LH concentration in May after the breeding season (LINCOLN et al. 1980). The data on nesting and sexual behavior were unfortunately not very detailed. Still, the raven, *Corvus corax,* is known to have a post-incubational peak in sexual activity and a pairbond which remains intact throughout the year (GWINNER 1964). A parallel exists then between the occurrence of sexual and courting activity and elevated levels of LH. In addition, the resurgence of sexual activity might have a role in the maintenance of the pairbond.

A relationship between LH and aggression is also possible as suggested by two results. First, the peaks of LH and aggression coincided. Secondly, after incubation both the LH plasma titers and the frequencies of aggressive

behavior were higher in male and female geese with goslings than in unsuccessful breeders. A number of authors have linked LH to aggression by altering the frequencies of aggressive behaviors and the dominance hierarchy in birds with the application of exogenous mammalian LH (Mathewson 1961; Davis 1963; Crook and Butterfield 1968; Lazarus and Crook 1973). The results on barheaded geese are only partly consistent with this hypothesis. This coincidences between LH and aggression peaks were not maintained over the whole year. Differences in LH titers disappeared before the molt, although significant differences in the frequency of aggressive behavior still existed.

LH can be summarized as having an important role in gonadal development. Some of the behavioral occurrences during the breeding season are reflected by changes in LH plasma titers. Incubation depresses the levels initially and having goslings produces a post-incubational peak. A parallel can be found between the occurrence of courtship behavior and elevated levels of LH although the amounts of courtship and LH are not proportional.

Seasonal changes in *prolactin* were pronounced. The patterns of changes were quite different in males and females.

In males, the peak values at the end of the breeding season might indicate a role in the decrease of steroid genesis and the regression of the gonads, as has been suggested by a number of authors (Nicoll 1974 and Ensor 1978 for reviews). Still, a negative effect of prolactin on LH concentration seems unlikely because both hormones were high at the end of the breeding season. Prolactin levels did increase while testosterone levels were decreasing or low. However, no significant negative correlation was found between the two on an individual basis. A similar positioning of the male prolactin maximum relative to gonadal growth, LH and testosterone was found in rooks (Lincoln et al. 1980). It can be concluded then that the antigonadal effect of prolactin is not a simple function of the plasma concentration.

A progonadal effect for prolactin has also been reported in males (see Ensor 1978 for a review). In ducks and two species of quail, the pituitary prolactin levels have been found to parallel the testicular cycles. In addition, Meier et al. (1971) found that stimulatory effects of gonadotrophic injections were enhanced by injections of prolactin when the two were separated by a 10-h interval. Prolactin levels in both adult male and female barheaded geese were elevated from March onwards. Progonadal effects can not be ruled out as increasing plasma titers of prolactin were found simultaneously with increasing LH and steroid levels.

High values of prolactin in females during incubation agree with the concept of its involvement in incubation (Nicoll 1974; Ensor 1978 for reviews). Elevated plasma concentrations of prolactin during nesting have been reported for Galliformes and waterfowl (Etches et al. 1979a, b; Sharp et al. 1979; Goldsmith and Williams 1980). The finding that brooding barheaded goose females have higher plasma titers after incubation than females without goslings is indirect evidence for the role of this hormone in incubation behavior. Two inferences can be made from the data. Peripheral levels of prolactin reflect incubation and brooding behavior, and the presence

of goslings can stimulate, or at least prevent the deterioration of brooding behavior and prolactin levels.

Other behavioral and physiological actions have been attributed to prolactin on the basis of exogenous hormonal injections. They include the control of migratory restlessness and fattening (MEIER et al. 1966) and feeding behavior (CHANDOLA and PAVGI 1979 and ENSOR 1978 for reviews). A comparison of prolactin curves with those for body weights and flight activity in barheaded geese demonstrates that neither migratory restlessness nor weight increases were related to increases in circulating prolactin.

The seasonal fluctuations of *thyroxine* were complex. For all classes of males and for subadult and juvenile females there were high levels in spring which decreased in fall. JOHN and GEORGE (1978) and CAMPBELL and LEATHERLAND (1980) found the same type of annual fluctuations in T4 in Canada geese and lesser snow geese. Adult females in this study and those investigated by CAMPBELL and LEATHERLAND had much more erratic annual cycles in T4 than the males. There were perhaps factors involved in egg production and incubation which affected the course of the annual curve. Other parameters like low temperature (JALLAGEAS et al. 1978; BOBEK et al. 1980), length of photoperiod (OISHI and KONISHI 1978; EL-SAYED et al. 1980) and time of the day (NEWCOMBER 1974) have been reported to affect thyroid function. Irregularities in females and also in males may then have represented a mixture of situational, seasonal and physiological effects.

Considerable evidence exists which links thyroid function and T4 to the timing of the molt (PAYNE 1972 for a review). This investigation as well as those mentioned above on geese have shown no relationship between T4 plasma concentrations and the primary molt. Recently, JALLAGEAS and ASSENMACHER (1974, 1979) proposed that the ratio of T4 to testosterone in plasma is a determinant factor in stimulating molt. T4 was reported to control the metabolic clearance rate of testosterone, and conversely oestrogens and androgens supposedly counteract the molt-inducing effects of thyroxine (KOBAYASHI 1958). The proposal may be applicable for barheaded geese males, as the ratio of T4 to testosterone was at a maximum just before the molt and remained high until October and November. The primary molt ended in August, but was followed by a body molt which lasted until fall.

In the same sense, an antigonadal and anti-androgen function has often been attributed to the thyroid (ASSENMACHER 1973 for a review; JALLAGEAS et al. 1978, 1979; ROBINZON and ROGERS 1979; PÊCZELY et al. 1980). Most of the evidence up to now has been gathered on males. Here too, in barheaded geese, the only relationship between peaks in thyroxine and decreases in testosterone were found in adult and subadult males. The absence of these effects in adult females, however, weakens the argument because they go through a gonadal regression and molt just as males.

As for prolactin, progonadal effects have also been reported for thyroxine, in addition to the antigonadal effects (JOHN and GEORGE 1978 for a review). A critical level of T4 has been proposed to be necessary for gonadal development. Both sexes of barheaded geese showed elevated levels of thyro-

xine during periods of gonadal development but no particular increases. A definitive relationship between thyroxine and pro- or antigonadal effects can not be determined from these data as an experimental approach is necessary to sort out the parameters involved in gonadal growth and regression.

The steroids *testosterone, DHT* and *oestradiol* are discussed together.

In testosterone, seasonal fluctuations were found in adult and subadult males and females and in juvenile males. The other androgen measured, DHT, had marked seasonal variations which were restricted to males. Oestradiol was only found in female plasma samples. The spring increases of testosterone, DHT and oestradiol were limited to less than a 2½-month period, in contrast to LH which was spread over a 4 to 5-month period. A similar pattern of LH and testosterone peaks has been shown for a number of bird species (Jallageas et al. 1978; Wingfield and Farner 1978 a, b; Lincoln et al. 1980; Donham 1979; Schwabl et al. 1981).

In adult males, peak levels of testosterone are most likely related with spermatogenesis (e.g. Brown and Follett 1977). Maximal levels for testosterone and DHT were found just before the females began to lay eggs. Levels in juvenile males were correspondingly lower, due to the immature nature of their testes.

In females, the testosterone maximum coincided with that of LH during egg laying. Increases of this kind have been shown to be directly associated with ovulation in chickens (Etches and Cunningham 1977; Johnson and van Tienhoven 1980). Donham (1979) and Wingfield and Farner (1978 a) reported similar testosterone peaks in field studies on mallards and white-crowned sparrows. Oestradiol has been shown to be involved in egg laying, as well as having a role in the development of the oviduct (Yu and Marquart 1973) which precedes egg laying. Consequently, the peak for oestradiol in barheaded geese occurred just prior to egg laying.

The data on juvenile females are of interest in regard to deferred maturity. Distinct increases in testosterone and oestradiol were present in their second fall. These increases preceded the females' being able to lay eggs in the following spring. It seems as though the factors which end the photorefractory period in adult females (see Farner and Follett 1979) have the effect of turning on steroid genesis in the immature ovary as both occur in the same time period.

In males, the relationship between sexual and courting behavior and testosterone has often been reported (Hutchinson 1976 for a review; Balthazart and Hendrick 1976; Gorman 1977; Pröve 1978; Wingfield and Farner 1978 a, b; Lincoln et al. 1980). Two types of information from the literature complicate the interpretation that androgens promote sexual and courting behavior in a proportional manner. In spring, the frequencies of sexual behavior do not always parallel plasma concentrations of androgens as has been reported by Gorman (1977). Secondly, in many species where autumnal peaks in sexual activity are present, only marginally elevated testosterone levels are found (Lincoln et al. 1980). The effects of androgens in fall would probably have to be mediated by increased receptor sensitivity in

the brain if the presence of androgens were solely responsible for promoting sexual behavior.

Complications of this type arose when examining the data on male barheaded geese. In spring, neither the decrease of sexual behavior during nesting nor the resurgence after incubation were reflected in plasma titers of testosterone or DHT. Subadult male levels were even lower than those of adults although they showed more courting behavior. Secondly, the autumnal increases in courting behavior were also not coincident with an increase in testosterone. The situation may be similar to that described by BALTHAZART and HENDRICK (1976). They found that by differentiating between displays directly related to copulation and those related to courtship, the frequency of sexual behavior could be shown to parallel the testosterone plasma titers in ducks. Courtship behavior was best related with the gonadotrophin FSH. In barheaded geese, copulatory and pre-copulatory behavior were limited to spring when testosterone levels were elevated. In fall, only courting behavior took place. Therefore, increased androgen concentrations may only be related to the occurrence of sexual behavior.

Testosterone has often been implicated in the control of aggressive behavior in males (BRAIN 1977 for a review; TEMPLE 1974; WINGFIELD and FARNER 1978 a, b; MOSS et al. 1979; SEARCY and WINGFIELD 1980). The data on barheaded geese provided only marginal support for the relationship between plasma titers of testosterone and the frequency of aggressive encounters. Levels of testosterone were slightly higher in successfully breeding males than in unsuccessful ones from August to November in accord with their higher frequencies of aggressive behavior. On the other hand, elevated values in intensive aggressive encounters occurred in July when testosterone levels were lowest. The relationship between circulating testosterone levels and the frequency of aggression is then complex.

In females, both oestradiol and testosterone have been reported to influence sexual and aggressive behavior (NOBLE 1972; KERN and KING 1972; WINGFIELD and FARNER 1978 a, b). The results on barheaded geese do not elucidate the matter. Both steroids showed elevated levels in the pre-incubational phases. The difference in the peaks is probably more related to physiological phenomena than the control of behavior. In fall, no differences were found between females with goslings, which were aggressive, and females without goslings.

To summarize, the only behaviors which appeared to be related to either androgen or oestrogen concentrations were sexual behavior and, in males, aggressive behavior outside of the breeding season.

*Corticosterone* plasma titers could not be examined on an annual basis because the effects of capture obscured any possible seasonal cycle. The results nonetheless demonstrated that an alarm situation can cause corticosterone plasma titers to increase. Simply watching other geese being caught stimulated the release of corticosterone. The levels were lower, and perhaps the amount of alarm was less in geese that were hand-raised and tame than in individuals raised in goose families. Although the effects of handling and alarm responses on corticosterone are well known in mammals (ADER 1969), they have often

been negated in birds (Culbert and Wells 1975; Etches 1976; Beuving and Vonder 1978; Eskeland and Blom 1979; Freeman and Manning 1979; Harvey et al. 1980).

In conclusion, a few points can be made about the relationship between behavior and hormones while considering the results presented here.

Sexual and aggressive behaviors are often discussed as being intrinsically related, or regulated by the same hormones in birds (Murton and Westwood 1977 for a review). The control of these behaviors is normally attributed to either androgens, especially testosterone, or to LH. A number of results from barheaded geese indicate that the relationships between LH, androgens, sexual behavior and aggressive behavior are complex. Subadults had extremely high levels in sexual and courting behavior but low levels in aggressive behavior without showing parallel trends in the circulating levels of the hormones measured. Secondly, the frequencies of intensive aggressive encounters in the flock were elevated in July while LH and testosterone were at their minimum annual values. Lastly, during incubation, the plasma titers of both hormones were high but the frequencies of attacks and sexual behavior were minimal.

These examples rather demonstrate that releasing factors like the presence of a female or the coming together of the flock can alter the frequency of behavior without effecting a lasting change in the circulating levels of hormones. On the other hand, short term effects can not be ruled out, especially in light of recent work by Harding and Follett (1979) which showed that aggressive encounters in birds can alter plasma titers of LH and androgens.

Comparing the data presented in this paper on LH to that of androgens, it seems that the gonadotropin was more sensitive with respect to changes in courting and aggressive behavior during the breeding season. The testosterone and oestradiol curves seemed to reflect better sexual behavior in males and females and in males the frequencies of attacks outside the breeding season. A synergistic action between the two hormones can not be ruled out because, in addition to steroids, protein hormones have also been found to bind in various parts of the brain (Krieger and Liotta 1979 for a review).

Seasonal control of behavior might also be related to changes in hormonal receptor concentrations in the brain or to selective activation of the receptors associated with various behaviors. In line with this, Barfield (1969, 1971) found that by implanting androgen into different parts of the brain, different behaviors could be elicited. Changes of this nature are outside the scope of the data on geese presented here. Still, the presence of comprehensive baseline data provides a good foundation for experimental analysis of these changes.

The results presented in this paper seem to support the following conception of behavioral control: Hormones may produce a propensity for an animal to behave in a certain way. However, social or situationally dependent factors act as releasers and can affect the frequencies of behaviors independent of the hormonal milieu of the individual. The presence of hormones is then not always a prerequisite for behavior, especially in animals which have a complex social structure.

## Summary

Seasonal changes in the following parameters were investigated in a free flying population of barheaded geese over three breeding seasons: the frequencies of pairbond displays, aggressive encounters, courting and sexual behavior, nesting and moulting records, and the circulating levels of LH, prolactin, T4, testosterone, DHT, 17 $\beta$-oestradiol and corticosterone.

The seasonal fluctuations were investigated with respect to differences between various social categories in the flock. Results showed that juveniles began to court later in the year than adults. Subadults courted more than any other age class. Pairbond displays and aggressive encounters were more frequent in successfully breeding adults outside of the breeding season than in unsuccessful breeders. LH increases occurred later in juvenile geese than in other geese. Successful breeders had higher levels of LH and prolactin directly after breeding than unsuccessful adults.

The annual cycle of each hormone was discussed in regard to other hormones, and physiological and behavioral effects. LH plasma concentrations were found to be positively related with testosterone and oestradiol. Elevated levels of LH occurred in periods where courtship behavior was frequent. Testosterone and oestradiol reflected more the occurrence of sexual behavior. Prolactin was found to be associated with incubating and brooding behavior in the female. Thyroxine was implicated in the control of the molt. Lastly, corticosterone levels were shown to be affected by alarm situations.



## Zusammenfassung

In einer frei lebenden Population von Streifengänsen wurden drei Brutperioden hindurch jahreszeitliche Schwankungen in folgenden Parametern untersucht: in der Häufigkeit von Paarbindungsverhalten, aggressivem Verhalten, Balzverhalten und sexuellem Verhalten, im Beginn und in der Dauer der Nistphase und der Mauser und in der vorhandenen Menge der Hormone LH, Prolaktin, T4, Testosteron, DHT, 17-Östradiol und Corticosteron im Blutplasma.

Die jahreszeitlichen Schwankungen in diesen Parametern wurden im Hinblick auf Unterschiede zwischen verschiedenen sozialen Klassen in der Schar untersucht. Juvenile Gänse begannen später im Jahr mit der Balz als adulte. Subadulte Gänse balzten häufiger als jede andere Altersgruppe. Ein Anstieg von LH zeigte sich bei juvenilen Gänsen später im Jahr als bei allen übrigen Klassen. Außerhalb der Brutsaison trat Paarbindungsverhalten bei erfolgreich brütenden Gänsen häufiger auf als bei Paaren ohne Bruterfolg. Direkt nach dem Brüten wiesen die erfolgreich brütenden Gänse einen höheren LH- und Prolaktinspiegel auf als erfolglose Paare.

Die Jahreskurve eines jeden Hormons wurde unter Berücksichtigung anderer Hormonkurven und der physiologischen Auswirkungen und Einflüsse auf das Verhalten diskutiert. Für Konzentrationen von LH im Plasma ergab sich eine positive Korrelation mit Testosteron und Östradiol. Ein Anstieg von

LH trat in Perioden mit vermehrtem Balzverhalten auf. Testosteron und Östradiol waren dagegen mehr mit dem Auftreten sexueller Verhaltensweisen verknüpft. Für Prolaktin konnte eine Beziehung zum Brutverhalten und Hudern der Weibchen nachgewiesen werden. Thyroxin spielte eine Rolle bei der Kontrolle der Mauser. Die Höhe des Corticosteronspiegels erwies sich als beeinflußbar durch Streßfaktoren.

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